

Title	Temporary loss of a sexual signal (claw loss) affects the frequency of sand structure construction in the fiddler crab,
Author(s)	Muramatsu, D.
Citation	Ethology Ecology & Evolution (2010), 22(1): 87-93
Issue Date	2010-02
URL	http://hdl.handle.net/2433/156175
Right	© 2010 Taylor & Francis Group.
Type	Journal Article
Textversion	author

**Temporary loss of a sexual signal (claw loss) affects the frequency of
sand structure construction in the fiddler crab, *Uca lactea***

D. MURAMATSU

Department of Zoology, Graduate School of Science, Kyoto University

Sakyo, Kyoto, 606-8502, JAPAN

muramatsu@ethol.zool.kyoto-u.ac.jp

Temporary loss of a sexual signal in fiddler crab

ABSTRACT

In iteroparous animals, individual decisions about when and how much to invest in reproduction are related to the lifetime reproductive success, and the ability to assess one's own competitive ability in one's current condition is necessary for optimizing the reproductive investment. Male fiddler crabs have an enlarged claw which is used for courtship and combat, but they sometimes lose the claw. The clawless males would have disadvantages in courtship and combat until they regenerated the claw. Here I examined whether males modify their reproductive investment in response to their current condition. Most clawless males did not construct sand structures to attract females; thus, they invested little in current reproduction. Small males were also less likely to construct structures. Clawless and small males may invest little in current reproduction and instead allocate energy to claw regeneration or body growth for future reproduction, or invest in an alternative mating tactics, surface mating.

KEY WORDS: fiddler crab, sand structure, claw, reproductive investment, energy allocation, *Uca lactea*

INTRODUCTION

Iteroparous animals are expected to have some degree of plasticity regarding their reproductive investment because there is a trade-off between current and future reproduction (Engqvist & Sauer 2002). Individual decisions about when and how much to invest in reproduction will be related to potential benefits in terms of offspring survivorship or mating success (Petrie & Williams 1993). To maximize the lifetime reproductive success, individuals would invest little in current reproduction and instead save resources when the potential benefits of reproduction were low (Tejedo 1992; Petrie & Williams 1993; Kvarnemo et al. 1995; Engqvist & Sauer 2002; Ruiz et al. 2008). Thus, it may be adaptive for individuals to assess their current competitive ability and the probability of reproductive success in order to optimize their reproductive investment. In the present study, I investigated how individuals adjusted their reproductive investment in response to the temporary loss of a male sexual signal in the fiddler crab, *Uca lactea*.

Fiddler crabs (*Uca*) are characterized by a single enlarged claw which grows on males. Males wave the large claw to attract females for mating (Zeil et al. 2006). However, there are some males that have lost their large claw in

natural populations (Yamaguchi 1973; Backwell et al. 2000; Reaney et al. 2007). These clawless males would be disadvantaged in courtship and combat until they regenerated their claw. Males regenerate their large claw in a relatively short time (4 months in *U. lactea*; Yamaguchi 1973), compared to their maximum life span (over 7 years in *U. lactea*; Yamaguchi 2002). Therefore, it may be adaptive for clawless males to avoid current reproductive investment and instead to conserve energy in favor of investment in claw regeneration for future reproduction.

Although males that have lost their large claw appear to be at a disadvantage for attracting females into their own burrows (burrow mating), males of *U. lactea* have an alternative mating tactic, surface mating, which does not require claw-waving (Yamaguchi 2001a). In surface mating, males visit females' burrows without vigorous waving, and copulate at the entrances to the females' burrows (Yamaguchi 1971, 1972, 2001a; Murai et al. 1987; Goshima & Murai 1988). Therefore clawless males may invest not only in claw regeneration but also in surface mating.

Male body size may also influence the investment in reproduction. If larger males are more successful at attracting females, large males would gain more benefit than small males with the same reproductive investment (Jennions & Backwell 1998). To maximize their lifetime reproductive success, small males may invest resources primarily in body growth.

Males of at least 18 species of fiddler crabs, including *U. lactea*, construct mud or sand structures at the entrance to their burrows (Christy & Backwell 2006), to which they attract females for mating (Christy et al. 2001, 2003a, b). Because surface mating does not involve male burrows, sand structures would not contribute to the mating success in surface mating. Thus sand structures would be constructed by the males that invest in burrow mating. The rate of structure construction varies among males (Backwell et al. 1995; Christy et al. 2001), and thus how much to invest in burrow mating differs individually. If the loss of their large claw and/or male body size affects mating success in burrow mating, they will change their reproductive investment, with clawless or small males constructing structures less frequently than intact or large males. I tested this prediction with *U. lactea* reproducing under the natural conditions.

METHODS

A field study was carried out in a dense colony of *U. lactea*, which was

approximately 3500 m² in area, centered on an intertidal mudflat in the estuary of the Yabusa River, Kagoshima, Japan (31° 41' N, 130° 17' E). Crabs emerged from their burrows and were active on the mudflat surface during the diurnal low tide. The entire study site was covered by the semidiurnal high tide, and sand structures constructed by crabs were destroyed by the tide.

Male crabs with and without intact large claws were captured from 25 May to 10 July 2005. To capture crabs, a wooden stick (1 m long, 1 cm in diameter) was used as a tool. One end of the stick was placed beside the entrance to the burrow, and I held the other end to control the stick. When crabs emerged from their burrows, I quickly moved the stick to obstruct the burrow entrance. Crabs were easily captured by hand after their way back into their burrows was blocked because they always tried to retreat into their own burrow to hide and never attempted any other means of escape.

For the random collection of crabs, I stuck a wooden pole (1 m long, 4 mm in diameter) vertically into the sediment, leaving approximately 5 cm above the surface, and I captured crabs possessing burrows beginning with the burrow closest to the pole. Crab-capturing was continued until most crabs were captured within a 1.5-m radius around the wooden pole. In addition, I searched for males that had lost their large claw and captured them whenever possible in order to collect enough samples of clawless males. Clawless males were distinguished from females, which have no large claw, by the feeding behavior (males use one claw, whereas females use both claws; Yamaguchi 2000) and the color of the left and right ambulatory legs (different color in males, same color in females; Yamaguchi 1971). To make it possible to relocate these burrows later, I stuck a sign pole near the burrow of each clawless male in the same way as described above.

After crabs were captured, their sexes were further confirmed by assessing the shape of their abdominal flaps, and their carapace width was measured with calipers to the nearest 0.05 mm. Crabs were marked by painting a number on their carapace for individual identification and released to their own burrows after they were kept for 10 to 15 minutes in a plastic cup to allow the paint to dry. If the paint became indistinct, the crab was captured again for repainting. The sizes of the smallest three males copulating on the mudflat were 7.85, 8.00, and 8.05 mm in carapace width. I therefore used 7.85 mm as the lower size threshold for reproductive males. To exclude immature males from the analyses, males smaller than 7.85 mm were disregarded.

To record the possession of structures, daily observation of the marked

males (intact and clawless) was conducted from 5 June to 3 August 2005 (which is their breeding season; Yamaguchi 2001b) except on rainy days. Observations were carried out after the time of lowest tide to ensure that most potential structure constructors completed construction. If intact males lost their large claw during the observation period, the data subsequent to claw loss were discarded.

The data were analyzed using glmmML (Generalized linear models with random intercepts; Broström 2008) in the statistical package R (R Development Core Team 2008). glmmML fits the model using maximum likelihood and numerical integration via the Gauss-Hermite quadrature (Broström 2003). Structure (constructed or not) was taken as the binary response variable, and as explanatory variables, possession of a large claw (presence or absence), carapace width of the focal males, and the interaction between these two terms were fitted. Binomial errors and a logit link function were used to analyze the data. To include individual variation in the model, I used individual identity as a random factor. I then selected the model that yielded the lowest Akaike's Information Criterion (AIC; see Akaike 1974) from all possible models with or without each term and interaction.

RESULTS

A total of 78 intact males and 47 clawless males whose carapace width exceeded 7.85 mm were marked (Fig.1). Sixty-three (80.8%) intact males and four (8.5%) clawless males constructed structures at least once during the observation period. The mean construction rate was 40.0% in intact males and 2.5% in clawless males. The smallest male that constructed a structure had carapace width of 11.00 mm.

In the glmmML analysis, the model that yielded the lowest AIC had possession of a large claw and carapace width as explanatory terms (Table 1). Loss of a large claw had a negative effect on the probability of structure construction, and there was a positive relationship between the probability of structure construction and carapace width (Table 2).

DISCUSSION

The results of the present study showed that the loss of a large claw had a negative effect on the probability of structure construction. This agrees with the

prediction that clawless males would invest little in structure construction. The fact that the four clawless males completed constructing structures indicates that males are physically capable of constructing structures without their large claw. Thus, it is presumed that clawless males abstain from constructing structures and thereby save energy for future reproduction. Males that have lost their large claw and cannot perform the claw-waving display may invest primarily in claw regeneration for future reproduction, perhaps because claw loss markedly reduces the probability of current reproductive success in burrow mating.

Another possibility is that clawless males invest primarily in surface mating. Because sand structure of *U. lactea* does not relate to surface mating (Muramatsu in press), investment in surface mating would not appear as the frequency of structure construction. Clawless males can copulate in surface mating without difficulty (Yamaguchi 2001a). Therefore clawless males may have invested in surface mating instead of saving energy for future reproduction.

Although some clawless males constructed structures, this study does not exclude the possibility that clawless males were physiologically unable to construct structures as frequently as intact males. Further investigations on the effects of claw loss on males are therefore needed.

Male competitive abilities that depend on their body size are expected to affect the individual reproductive investment. Indeed, my data showed that the carapace width of males and the probability of structure construction were positively related in my data. Large males may be dominant in courtship and invest more in reproduction, or costs associated with burrow mating or structure construction may be prohibitive for small males.

In the separate study, I showed that the possession of a structure is costly for burrow owners and some males even destroy their own or experimentally planted structures (Muramatsu 2009). Sand structures are able to attract females (Christy et al., 2001, 2003a, b), but the structures may also attract males and non-receptive females (Backwell et al., 1995; Christy et al., 2003b) because sand structures function as "sensory traps," which exploit the predator-avoidance response of the crabs to entice them into the males' burrows (Christy et al., 2003a, b). Small or clawless males may not be able to repel intruding crabs and hence they can not afford to construct structures.

ACKNOWLEDGEMENTS

I would like to thank M. Imafuku and A. Mori for providing constructive comments on the manuscript. I also thank E. Nakajima, S. Cook, and S. Barribeau for revising the English. This research was financially supported in part by the Global COE Program A06 to Kyoto University.

REFERENCES

- Akaike, H.** 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19: 716-723.
- Backwell, P. R. Y., Jennions, M. D., Christy, J. H. & Schober, U.** 1995. Pillar building in the fiddler crab *Uca beebei*: evidence for a condition-dependent ornament. *Behavioral Ecology and Sociobiology* 36: 185-192.
- Backwell, P. R. Y., Christy, J. H., Telford, S. R., Jennions, M. D., & Passmore, N. I.** 2000. Dishonest signalling in a fiddler crab. *Proceedings of the Royal Society of London, Series B* 267: 719-724.
- Broström, G** 2003. Generalized linear models with random intercepts. <http://www.stat.umu.se/forskning/reports/glmmML.pdf>.
- Broström, G** 2008. The glmmML Package. <http://cran.r-project.org/web/packages/glmmML/glmmML.pdf>.
- Christy, J. H. & Backwell, P. R. Y.** 2006. No preference for exaggerated courtship signals in a sensory trap. *Animal behaviour* 71: 1239-1246.
- Christy, J. H., Backwell, P. R. Y. & Goshima, S.** 2001. The design and production of a sexual signal: hoods and hood building by male fiddler crabs *Uca musica*. *Behaviour* 138: 1065-1083.
- Christy, J. H., Backwell, P. R. Y. & Schober, U.** 2003a. Interspecific attractiveness of structures built by courting male fiddler crabs: experimental evidence of a sensory trap. *Behavioral Ecology and Sociobiology* 53: 84-91.
- Christy, J. H., Baum, J. K. & Backwell, P. R. Y.** 2003b. Attractiveness of sand

hoods built by courting male fiddler crabs, *Uca musica*: test of a sensory trap hypothesis. *Animal Behaviour* 66: 89-94.

Engqvist, L. & Sauer, K. P. 2002. A life-history perspective on strategic mating effort in male scorpionflies. *Behavioral Ecology* 13: 632-636.

Goshima, S. & Murai, M. 1988. Mating investment of male fiddler crabs, *Uca lactea*. *Animal Behaviour* 36: 1249-1251.

Jennions, M. D. & Backwell, P. R. Y. 1998. Variation in courtship rate in the fiddler crab *Uca annulipes*: is it related to male attractiveness? *Behavioral Ecology* 9: 605-611.

Kvarnemo, C., Forsgren, E. & Magnhagen, C. 1995. Effects of sex ratio on intra- and inter-sexual behaviour in sand gobies. *Animal Behaviour* 50: 1455-1461.

Murai, M., Goshima, S. & Henmi, Y. 1987. Analysis of the mating system of the fiddler crab, *Uca lactea*. *Animal Behaviour* 35: 1334-1342.

Muramatsu, D. 2009. To build or not to build – or to destroy burrow hoods in a population of *Uca lactea*. *Journal of Crustacean Biology* 29: 290-292.

Muramatsu, D. (in press). Sand structure construction in *Uca lactea* (De Haan, 1835) is related to tidal cycle but not to male or female densities. *Crustaceana*.

Petrie, M. & Williams, A. 1993. Peahens lay more eggs for peacocks with larger trains. *Proceedings of the Royal Society of London, Series B* 251: 127-131.

R Development Core Team 2008. R: A language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna* (<http://www.R-project.org>).

Reaney, L. T., Milnera, R. N. C., Dettoa, T. & Backwell, P. R. Y. 2007. The effects of claw regeneration on territory ownership and mating success in the fiddler crab *Uca mjoebergi*. *Animal Behaviour* 75: 1473-1478.

Ruiz, M., Davis, E. & Martins, E. P. 2008. Courtship attention in sagebrush lizards varies with male identity and female reproductive state. *Behavioral Ecology* In Press.

Tejedo, M. 1992. Large male mating advantage in natterjack toads, *Bufo calamita*: sexual selection or energetic constraints? *Animal Behaviour* 44: 557-569.

Yamaguchi, T. 1971. Courtship behavior of a fiddler crab, *Uca lactea*. *Kumamoto Journal of Science* 10: 13-37.

Yamaguchi, T. 1972. Ecology of a fiddler crab (*Uca lactea*), (2) Courtship and mating behaviors. *Calanus* 3: 38-53.

Yamaguchi, T. 1973. Asymmetry and dimorphism of chelipeds in the fiddler crab, *Uca lactea* De Haan. *Zoological Magazine* 82: 154-158.

Yamaguchi, T. 2000. Sexual differences in feeding by the fiddler crab, *Uca lactea* (De Haan). *Crustacean Research* 29: 121-132.

Yamaguchi, T. 2001a. The mating system of the fiddler crab, *Uca lactea* (Decapoda, Brachyura, Ocypodidae). *Crustaceana* 74: 389-399.

Yamaguchi, T. 2001b. The breeding period of the fiddler crab, *Uca lactea* (Decapoda, Brachyura, Ocypodidae). *Crustaceana* 74: 285-293.

Yamaguchi, T. 2002. Survival rate and age estimation of the fiddler crab, *Uca lactea* (De Haan, 1835) (Decapoda, Brachyura, Ocypodidae). *Crustaceana* 75: 993-1014.

Zeil, J., Hemmi, J. M., & Backwell, P. R. Y. 2006. Fiddler crabs. *Current Biology* 16: 40-41.

Table 1: AIC ranking of the generalized linear mixed models explaining the probability of structure construction.

Ranking	Model term(s)	AIC
1	Claw, size	1281
2	Claw	1282
3	Claw, size, claw*size	1282
4	Size	1341
5	None	1342

"claw" indicates the possession of a large claw, "size" indicates carapace width of males. An asterisk between terms denotes interaction.

Table 2: Maximum-likelihood estimates and their standard errors for each term in the selected lowest AIC model explaining the probability of structure construction.

Model term	Estimate	SE
intercept	-3.163	1.568
claw(lost)	-3.586	0.566
size	0.175	0.105

"claw(lost)" indicates the absence of a large claw, "size" indicates carapace width of males.

FIGURE LEGEND

Figure 1: Relationships between the rate of structure construction and carapace width of intact and clawless males.

Each symbol represents one individual. Circles represent males that had an intact large claw. Diamonds indicate males that had lost their large claw. The size of each symbol reflects the category of the corresponding sample size (number of observed days); less than 5 times, 5 to 19 times, and more than 20 times.

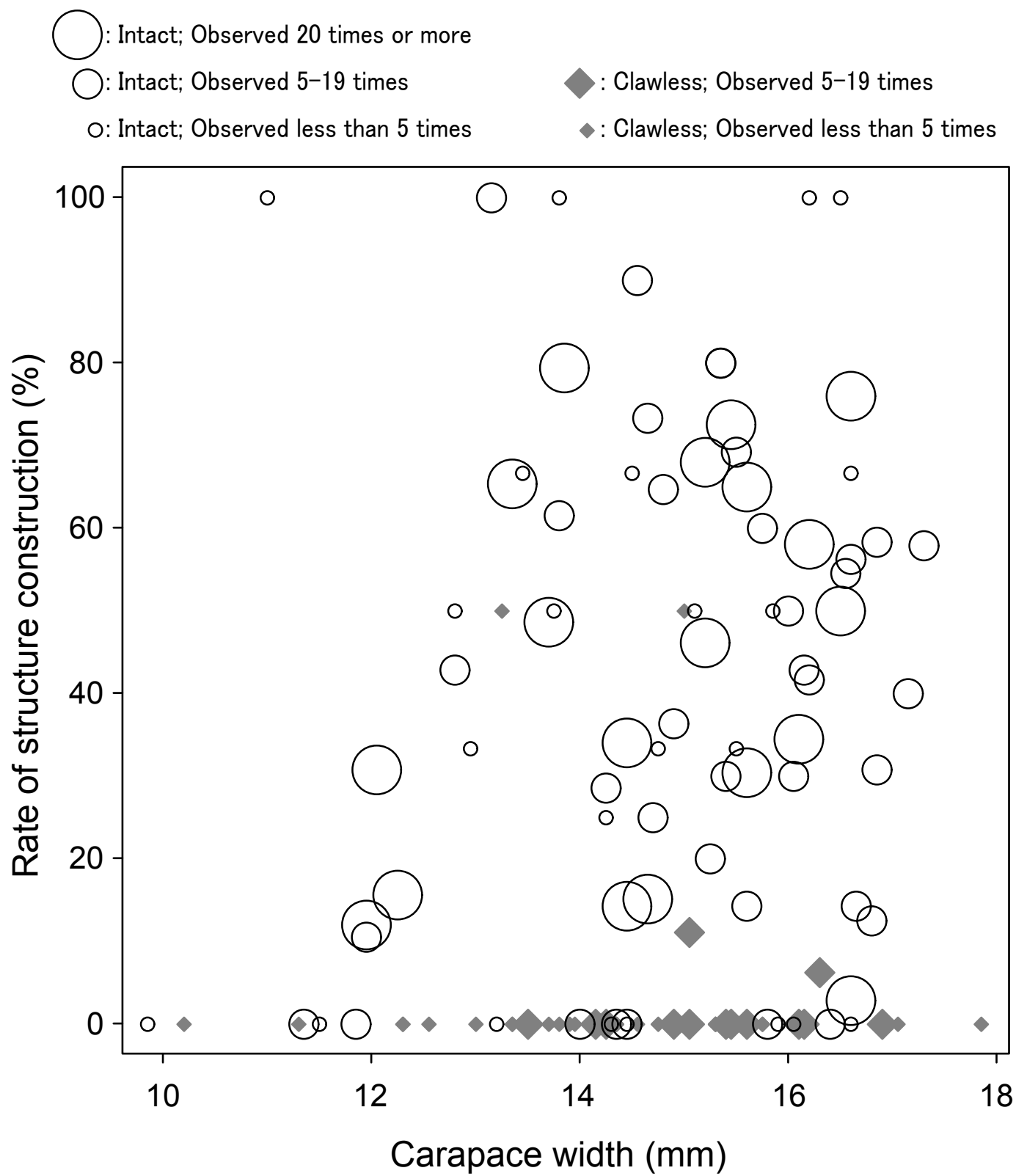


Fig. 1